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# THE SELECTION PROBLEM[1]

RAYMOND PEARL

OF all the supporters of the doctrine of natural selection as the chief factor in organic evolution, August Weismann was preeminent. He stood shoulder to shoulder with Wallace in his entire willingness to attempt the explanation by selection of any biological phenomenon whatsoever, and he far outstripped the latter in the keenness and subtlety of his logical powers when an especially difficult bit of exegetic activity was called for. Both, it hardly needs saying, left Darwin far behind in the extent of their advocacy of the *Allmacht* of selection. Certain it is that if any one could speak authoritatively, and without suspicion of either hostility or doubt, about the selection theory, Weismann could. For that reason it seems desirable to take as the starting point of this discussion a statement made by that distinguished biologist so lately as seven years ago. At the Darwin Centenary meeting in Cambridge, Weismann, discussing the adequacy of the selection theory to explain the initial steps of evolutionary change, said:[2]

> To this question even one who, like myself, has been for many years a convinced adherent of the theory of selection, can only reply: *"We must assume so, but we can not prove it in any case.* It is not upon

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[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station No. 109. This paper constitutes the address of the retiring President, read in abbreviated form at the dinner of the American Society of Naturalists in New York, December 29, 1916.

[2] ''Darwin and Modern Science,'' Cambridge, 1909, p. 25. The italics are in the original.

demonstrative evidence that we rely when we champion the doctrine of selection as scientific truth; we base our argument on quite other grounds."

Even since 1909 a good deal of water has flowed under all our bridges, and particularly under the evolutionary ones. Among other changes in viewpoint there is evident a marked disinclination in science nowadays to regard as "scientific truth" anything which is not based upon demonstrative evidence. But it is also a fact, perhaps at first thought to be regarded as curious, in view of the opinion of Weismann which has been quoted, that there are here with us to-day those who assert, with great zeal and pertinacity, that in selection is to be found the chief cause of evolutionary change. These things being so, it has seemed that possibly it might be profitable to spend a little time upon the selection problem, trying to determine whether the case is any better now than Weismann conceived it to be seven years ago, from the viewpoint of tangible objective evidence. It is to be hoped that it is, for among working geneticists just now any theory which has to depend for its sole support upon its "interpretative value"[3] is sure to receive scant attention.

So then what I shall try to do is to review briefly some of the real evidence about the selection problem which has been accumulating since biologists turned definitely to the experimental study of evolution, and definitely away from the glorious, but on the whole unproductive, attempt to solve its problems by *a priori* reasoning. From such a review it is to be hoped that we may get some light as to the directions in which further research and new evidence are most urgently needed.

## I. NATURAL SELECTION

In considering the whole selection problem we may well begin with an examination of the theory of natural selection. The mere fact of natural selection, in the sense solely and strictly of a process leading to the elimination of some individuals and the survival of others, is no longer questioned by any one who takes the trouble either to think or to observe living things. It is a process which goes on constantly and affects all organisms. In this sense it is no more than the resultant of the observed absence of individual, mundane immortality among living things. The fact that individuals die implies that those not yet dead are a selected lot, in at least one respect, namely survival.

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[3] Weismann, *loc. cit.*, p. 50.

This mere fact of elimination and survival is, however, not in itself particularly illuminating. The first question before us is whether such a process is capable of bringing about evolutionary changes of a progressive sort. Obviously it is capable of doing so, in theory at least, if we add two assumptions, or better rules according to which the Dance of Death is to be performed. The first of these rules is that the individuals alive at any time shall be different from those dead, in some other respects than that of survival merely. In other words, the elimination shall be selective. The second rule is that the survivors shall transmit to their progeny those differences which mark them off from the eliminated. The theory that these two rules are always and everywhere in operation, taken together with the observed fact that living creatures do die, *is* the Darwinian theory of natural selection as a factor in organic evolution. If the premise be granted that the game of survival is in fact played by these rules, the conclusion is then logically irresistible that evolutionary progress is bound to occur in the direction of those differences which distinguish the survivors.

Here many have been content to let the matter rest. In the minds of an astonishingly large number of people, which number includes some rather great names in the world of science, it is precisely the same thing to show that something logically must be so, as it is to show that it is so. If the formal rules of logic are satisfied, truth seems to them to be thereby established. No further evidence is demanded. As every one knows, this attitude led practically to the intellectual bankruptcy of the whole evolution theory in the late nineties, from which it was rescued only by the active movement towards an objective, experimental accumulation of facts about the subject. But the danger which lurks in formal logic is always threatening the progress of science. In the field of science in which we are interested the most recent conspicuous example of it is found in the vicious attacks on Mendelism, which upon analysis can be seen to have their only basis in a formally logical, so-called "proof" that it can not be true. The danger is so insidious, and takes such diverse forms, that one feels justified in quoting a brief statement made by Professor F. C. S. Schiller,[4] which might well, in sufficiently large type, be hung upon the wall of every biological laboratory, as a constant reminder that the foundations of scientific truth lie in experiment and observation, not in logic. Schiller says:

> The proof that any logic, which declines to consider the question of the real truth of the reasonings it attempts to deal with, necessarily condemns itself to utter formality is easily given, and very instructive. It is a formal characteristic of *every* assertion that it *claims truth,* absolutely and without reservation or suggestion of fallibility. Hence it follows both if (*a*) the question of the actual value of this claim is ruled out of order, and if (*b*) the assertion is accepted at its own estimation, that the distinction between true and false must, in fact though not in name, disappear from Logic. For all assertions will be held true because they formally claim truth; because none profess to be false, error no longer exists—for Logic. Thus the logical form of an assertion affords no means of deciding upon the real value of its claim to truth, and hence any logic which restricts itself to the study of this form inevitably accepts a truth-claim as the equivalent of real truth. It is like a bank which does not distinguish between promises to pay and hard cash.

Then clearly the question to which we want an answer is not whether natural selection *can* cause evolutionary changes, but rather whether it *does* cause such changes in any significant degree or extent. In other words, we shall prefer the "hard cash" of objective experimental evidence to any logical "promise to pay," however tight and compulsive its reasoning.

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[4] Schiller, F. C. S., "Formal Logic. A Scientific and Social Problem." London, 1912, pp. 6–7.

The tale here is not a long one. Indeed it is surprisingly brief, considering the mass of literature which the theory of natural selection in its more formally logical aspects has engendered. We have first the pioneer work of Weldon[5] with *Carcinus,* in which a selective elimination of individuals different physically from the survivors was first demonstrated numerically, the eliminating environmental factor being the silt in the water. This was followed by a number of investigations of a more or less similar character, notably those of Poulton and Sanders[6] with *Vanessa,* and of di Cesnola[7] with *Mantis,* in which different colored forms of these insects were exposed to elimination by natural enemies, chiefly birds, with the result that there was found to be some relation between the chances of elimination and the degree to which the insect matched its background. Bumpus[8] studied surviving and eliminated English sparrows after a severe winter storm. Crampton[9] measured the surviving and eliminated pupæ of *Philosamia,* the elimination having been produced by wholly natural causes. Davenport,[10] in a very small lot of chickens, found that those killed by crows were colored differently from those eliminated. Lutz[11] found in *Drosophila* some differences in type between survivors and eliminated. Harris[12] has shown that among seedling beans abnormal types perished more frequently than strictly normal types under the same field conditions. The same author[13] has also made extended researches on the elimination of organs in a series of different plants.

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[5] Weldon, W. F. R., *Proc. Roy. Soc.,* Vol. XLVII, pp. 360–379, 1894. Also see Brit. Assoc. Rept., Bristol (1898), pp. 887–902, 1899.

[6] Poulton and Sanders, Rept. Brit. Assoc. (Bristol), pp. 906–909, 1899.

[7] di Cesnola, A. P., *Biometrika,* Vol. III, pp. 58–59, 1909.

[8] Bumpus, H. C., Biological Lectures, Woods Hole, 1908, pp. 209–226, Boston, 1899.

[9] Crampton, H. E., *Biometrika,* Vol. III, pp. 113–130, 1904.

[10] Davenport, C. B., *Nature,* Vol. LXXVIII, p. 101, 1908.

[11] Lutz, F. E., *Bulletin Amer. Mus. Nat. Hist.,* Vol. XXIV, pp. 605–624, 1915.

[12] Harris, J. A., *Science,* N. S., Vol. XXXVI, pp. 713–715, 1912.

[13] Harris, J. A., *Science,* N. S., Vol. XXXII, pp. 519–528, 1910. *Pop. Sci. Monthly,* Vol. LXXVIII, pp. 521–538, 1912, and numerous other papers in *Biometrika,* AMER. NAT. and elsewhere.

The critical value of these different investigations is not in every case equal. Some are distinctly fragmentary, and in others the differences between eliminated and surviving are so small as to be of extremely doubtful significance. If one examines critically the actual biometric constants in the more extended of these studies (*e. g.*, Crampton's and Bumpus's as analyzed by Harris[14]) he can not but be impressed with the doubtfulness of many of the differences. However, if we take all these researches at their face value, and give all the benefit of the doubt to the weak, then they agree in indicating that the survivors are of somewhat different type physically than the eliminated.

But nearly as many investigations have been made which show that, on the whole, the survivors are not physically different from those naturally eliminated. Again the studies of Weldon[15] on *Clausilia* come first. Closely related to these is di Cesnola's[16] work on *Helix*. All three of these investigations agree in showing no significant difference in physical type between the general population before elimination and the selected survivors from that population after elimination. There was in *Helix* and in *Clausilia laminata* some reduction in variability, but even that failed in another species of *Clausilia*. Kellogg and Bell[17] were not able to find any evidence that survivors and eliminated were different in respect of either type or variability under natural conditions, in the case of bees, or of the lady-bird beetle *Hippodamia*. Pearl,[18] in a much more extended series of observations than those of Davenport, found no relation between the colors of chickens and their elimination by natural enemies. This result, it may be said, has been confirmed in subsequent years. Reighard,[19] in one of the most beautiful experimental studies of natural selection which has ever been made, found that there was no relation between the colors of coral, reef fishes and their elimination by natural enemies.

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[14] Harris, J. A., AMER. NAT., Vol. XLV, pp. 314–318. 1911.

[15] Weldon, W. F. R., *Biometrika*, Vol. I, pp. 109–124, 1901, and *Ibid.*, Vol. III, pp. 290–307, 1904.

[16] di Cesnola, A. P., *Biometrika*, Vol. V, pp. 387–399, 1907.

[17] Kellogg, V., and Bell, R. G., *Proc. Washington Acad. Sci.*, Vol. VI, pp. 203–332, 1904.

[18] Pearl, R., AMER. NAT., Vol. XLV, pp. 107–117, 1911.

While the researches which have been mentioned do not exhaust the literature, they are all for which time can be spared now, and they are fairly representative of the whole of the distinctly meager experimental and quantitative evidence regarding selective elimination. On the whole, the net result is not so clear-cut and outstanding as could be wished. If a scientific person came here from some other planet with an earnest desire to inform himself about selective elimination, of which he had not before known anything, and read all the available real evidence on the point, he would be sure to come to some such conclusion as this: that in some cases natural elimination is certainly in some degree selective, while in other cases it certainly is not; and in the most favorable cases of all the selection is apparently not very rigorous. Grossly teratological abnormalities are eliminated. But the smaller deviations from type, which in theory ought to furnish the basis of selection, appear upon quantitative study less generally and sharply determinative of survival than might reasonably have been expected theoretically. The case regarding this first element of the theory of natural selection certainly seems far less strong, under the critical eye of experiment and measurement, than those of us who were nourished on Weismann, Romanes, and their like, would have supposed possible twenty years ago. Still the writer has no desire to be controversial about the matter and if any one is disposed to draw the opposite conclusion from the facts he is entirely welcome to.

Let us now turn to the consideration of our second rule, which must be fully enforced if natural selection is to be an important factor in the causation of evolutionary change. This, it will be recalled, was that the survivors must produce offspring which bear characters like those which had led to the survival. Or, to put the matter crudely, the survivors must transmit their characters to their offspring. In pre-Mendelian days this phase of the subject was always neatly and summarily disposed of by stating, as one of the *facts* on which the theory of natural selection rested, that "variations are inherited" or "like produces like." Times have changed. We are a great deal less certain about that particular brand of inheritance which the theory of natural selection demands than we were before any one had taken the trouble to make experiments on heredity. The essential difficulty lies here. The differences upon which natural selection directly operates are somatic differences, by hypothesis and in fact. Every worker in genetics has learned since the truly epoch-making researches of Johannsen[20] to be extremely cautious in assuming *a priori* that any particular somatic difference is so inherited.

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[19] Reighard, J., Carnegie Institution, Publication 103, pp. 257–325, 1908.

The writer has lately been experimenting with a character which very well illustrates this point. A not infrequent variation of the single comb in poultry is the appearance, on one or both sides of the comb, of a small excrescence, known technically as a side-sprig. Individuals exhibiting this variation have been selected for breeding purposes. But, so far as the experiments have yet gone, it does not appear that the offspring of such animals are any more likely to exhibit the variation than are the offspring of any random sample of single-combed fowls. Now suppose, for a moment, that in a state of nature the possession of a side-sprig on the comb gave a bird a distinctly better chance for survival than did a plain single comb. Those lacking the variation would then by hypothesis tend to be eliminated, but there is not the smallest indication that there would result any progressive evolution towards a side-sprigged race.

Now one might go on and review a great accumulation of evidence from the work of de Vries,[21] Dewar and Finn,[22] Bateson,[23] Lloyd,[24] and many others, showing the failure of the theory of natural selection to account satisfactorily for various observed happenings in evolution. It is not my purpose to do this. These facts are all familiar, and indeed have become commonplaces of biological literature. We may, however, with some chance of profit try to generalize all this evidence. If we do so, the writer believes that the conclusion will be reached that natural selection is no longer generally regarded as the primary, or perhaps even a major, factor in evolution because of three general groups of facts, each well established by the common observation of many biologists. The first of these large facts is that all organisms possess in varying, but usually very large, degree the power of personal, immediate, individual, somatic adaptation to the environment. In consequence of this power of personal adaptation the survival expectation of an individual is not generally and regularly a function of any static, single-valued relation between its somatic structure, habits, or physiology, on the one hand, and the impinging environmental stresses on the other hand. Yet such a relation is implicitly assumed in that part of the theory of natural selection which affirms a selective elimination on the basis of somatic characteristics. The second broad fact is that, even when selective elimination on the basis of somatic characteristics does occur, it does not follow generally and regularly that the somatic differences on which the selection acted will reappear in the progeny, or in short be inherited, actual experience having abundantly demonstrated that a very great many of such somatic differences are not inherited. The third large fact is that observation indicates that in many cases evolutionary changes have come about by relatively large, discontinuous steps, the new form being not merely fully differentiated at its first appearance, but also fully able to survive.

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[20] Johannsen, W., "Ueber Erblichkeit in Populationen und in reinen Linien." Jena, 1903.

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[21] de Vries, H., "The Mutation Theory." Chicago.

[22] Dewar, D., and Finn, F., "The Making of Species." London.

[23] Bateson, W., "Problems of Genetics." New Haven, 1913.

[24] Lloyd, R. E., "The Growth of Groups in the Animal Kingdom." London, 1912.

Natural selection is, from the point of view of modern genetics, a somatic theory. It begins and ends in somatic differences. Except under the most unusual and rare of conditions natural selection can not possibly operate *directly* upon germ-cells. It must, from the very nature of the case, work only indirectly upon the germ through the soma. Now it is a historical fact that just so long as the study of heredity confined itself solely to the somatic results of the process, substantially no advance in knowledge was made. Only when it was clearly perceived that heredity is primarily and fundamentally a problem in the physiology of *germ cells,* and that the soma is, as some one has said, only the mechanism which the fertilized egg uses to produce another fertilized egg like itself, did we begin to make progress. Can we suppose that these considerations have no meaning or application in our attempts to solve the larger problem of organic evolution?

If natural selection only could act directly upon germ cells we should have a different story to tell. The writer has lately been experimenting[25] with an agent which acts with extraordinary precision and definiteness in a selective manner upon the germ cells, killing or inactivating the weak, and leaving only the strong and resistant to produce zygotes, and somata. This substance is alcohol. In the case at least of the domestic fowl the evolutionary effects produced by this substance are remarkable in their magnitude and definiteness. It is not possible here to go into details, but briefly it may be said that the first general result of the continued administration of ethyl or methyl alcohol, by the inhalation method, to the parents in poultry, is to diminish progressively the fertility. But the smaller number of offspring formed by the surviving germ cells, after selective elimination in the gonads has occurred, are in every measurable respect distinctly and markedly superior to the normal individuals of the races from which they come. Here is *real* selection making *real* evolutionary progress, because its point of application is the germ and not the soma. That the same agent may produce an evolutionary change in the opposite direction in another organism, the guinea pig, as has been shown by Stockard[26] to be the case, seems to mean, from the point of view of the present discussion, nothing more than that the direction and amount of any evolutionary change is, fundamentally, a function of two variables, the organism and the environment. If the same environmental stress produced the same evolutionary effect upon all organisms, then it would follow that all organisms in the same environment must necessarily be alike at the end of the process, which is, of course, not the case.

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[25] Pearl, R., *Proc. Amer. Phil. Soc.*, Vol. LV, pp. 243–258, 1916; *Proc. Nat. Acad. Sci.*, Vol. 2, pp. 380–384; *Ibid.*, Vol. 2, pp. 675–683, 1916; *Jour. Exper. Zool.*, Vol. 22, 1917.

## II. THE EXPERIENCE OF PRACTICAL BREEDERS

Let us at this point leave our discussion of natural selection and turn to the other great aspect of the problem, artificial selection. Here we shall tread on surer ground, first, because it is where the great bulk of the experimental work on the selection problem has been concentrated, and second, because the considerable mass of reliable historical material about the origin and improvement of domestic animals and plants becomes available as a source of pertinent and critical evidence on the problem. At the outstart it may be recalled that it was on the supposed results of artificial selection, as set forth in the experience of practical breeders, that Darwin chiefly relied for objective evidence in favor of natural selection.

In general this evidence has been accepted very uncritically by followers of Darwin. This is not strange in view of the fact that there have been, and are now, relatively few trained biologists who know anything at first hand about the practical breeding of animals for the show ring, advanced registry test, or any other purpose which involves necessarily the production of élite specimens which shall rank measurably with the best of the breed.

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[26] Cf. Stockard, C. R., and Papanicolaou, G., AMER. NAT., Vol. 50, pp. 65–88, 144–177, 1916.

This fact has led to some entirely unwarranted inclusions in the technical literature of biology. Statements in the agricultural press which were intended by their breeder-authors merely as harmless generalities on a subject about which they had not the slightest intention of being specific, have been accorded, by the laboratory evolutionist, the dignity and authority of detailed reports of actual breeding operations, and cited as valuable evidence on the problem of evolution.

This confusion has played particular havoc in discussions of the selection problem because of the general and usually quite irresponsible use of the term "selection" by practical breeders. In the literature of live stock breeding the word "selection" has been, and is being used to-day, to designate, upon occasion, every known kind of breeding operation. To illustrate: a fancier who bred a new variety of poultry started with a mongrel male bird which happened to possess just the combination of characters which he wanted in his new breed, as the result of a previous series of indiscriminate crossings. This male was crossed with a female of a well established breed which possessed some of the desired characters. The daughters from this mating were back-crossed to their sire, the original male bird, and so in turn were his granddaughters. The granddaughters' progeny constituted the new breed, full blown and breeding tolerably true. This was an entirely legitimate, and indeed usual, way of making a new breed. But the point lies in the fact that the breeder who did all this always refers publicly to the series of matings which has just been described as "this process of *selection*"!

Since Darwin selection has been a word to conjure with amongst the practical breeders. In most cases without any comprehension whatever of the exact technical sense in which the term was originally used breeders have taken the word itself as a sort of fetish. Darwin[27] himself speaks of artificial selection as "the accumulation in one direction, during successive generations, of differences absolutely inappreciable by an uneducated eye." Men in whose breeding operations selection in this sense demonstrably plays no significant part whatever, attribute to its magic power all improvement in their animals and plants. This is harmless so long as one understands that the "selection" is verbal and not biological. But unfortunately it has not always been so understood. Consequently we find the literature of evolution cluttered with a lot of utterly preposterous statements about domestic animals and plants, masquerading as valid evidence for the selection doctrine.

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[27] Darwin, C., "Origin of Species," Chap. I, p. 26.

So fixed in the minds of most biologists not acquainted with agricultural matters at first hand is the idea that the vast majority of improved varieties of plants and animals owe their origin, or their improvement, or both, to cumulative selection of slight differences, that it appears desirable to review briefly a few of the actual facts. One can not hope to do more than touch here and there in a great body of evidence, but at least representative cases may serve to indicate the general tenor of the whole.

We may consider first the cultivated grape, of which there are over 1,300 recognized varieties grown in this country. Hedrick[28] and his assistants have made a very careful and systematic study of the origin of these forms. After discussing the early history of the vine in this country he says (p. 52):

> We have found that the wild grapes of the country, valued but uncultivated for two hundred years, became through mere transplanting from the woods into the vineyards . . . one of our most important fruits.

Again in commenting upon the growth of the grape-growing industry he says (p. 62):

> The results achieved seem all the greater when one considers that many of the best varieties now grown are the first, and scarcely any are further removed than the second generation from wild plants.

But we should not be content with these general statements. Let us examine specifically the history of a well-known and very excellent "improved" variety, the Concord. Of this grape Hedrick says (p. 219):

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[28] Hedrick, U. P., "The Grapes of New York." Albany, 1908.

> The Concord is known by all. The most widely grown of the grapes of this continent, it also represents the dominant type of our native species and with its offspring, purebred and crossbred, furnishes seventy-five per cent. or more of the grapes of eastern America.

He speaks of "the preeminently meritorious character of Concord which has enabled it to take first place in American viticulture."

Now for the origin and history of this paragon.

> The seed of a wild grape was planted in the fall of 1843 by E. W. Bull of Concord, Massachusetts, from which fruit was born in 1849. The wild grape from which the seed came had been transplanted from beside a field fence to the garden in which there was at least another grape, the Catawba, and the wild vine was open to cross-pollination. One of these seedlings was named Concord and the variety was exhibited before the Massachusetts Horticultural Society in the fall of 1852. The new grape was introduced in the spring of 1854 by Hovey & Company, of Boston. From the time of its introduction the growth of this variety in popularity was phenomenal. In 1865 it was awarded a prize by the American Institute . . . as the best grape for cultivation.

But where in the history of this "best" American grape is the gradual accumulation of minute variations by selection? The story is of the same sort for all varieties of grapes about whose origin anything is known; either they were chance seedlings, or $F_1$ hybrids, or $F_2$ segregates, grown under good conditions.

The same general situation obtains in regard to the origin and improvement of other fruits besides the grape. One need only mention various cases briefly to recall them to mind. New and improved varieties of apples, plums, cherries, strawberries, etc., have originated either as chance seedlings, or as bud variations, or as hybrids. In their production selection, in the sense of the accumulation of minute favorable variations, has had no part.

In the case of many fruits the mere fact of domestication accounts for all the improvement over the wild type. A striking example of this is found in the case of the most recently domesticated wild plant, the blueberry. Mr. F.

V. Coville[29] succeeded in discovering some years ago the two essentials for the successful cultivation or domestication of the swamp blueberry (*Vaccinium corymbosum*). These were found to be (1) an acid soil, and (2) a root fungus that appears to supply the plant with nitrogen. When these essentials are supplied, and the plant brought under cultivation, a marked improvement in the size and quality of the berries at once occurs. Further improvement is being made by hybridization, and by seeking superior natural variations to be used in such hybridization and for asexual propagation. In his latest paper Coville makes this statement, the significance of which in the present connection will be noted.

> Seedling plants, even from the largest berried wild parents, produce small berries as often as large ones.

Selection, in the Darwinian sense, is playing no part in the improvement of the blueberry, so far as we can learn from the published records. The essential factors in the improvement are better conditions, hybridization, and the asexual propagation or superior natural variations.

Let us now turn to other sorts of plants. In 1910 my colleague, Dr. Frank M. Surface, originated a variety of oats, known as Maine 340, which is superior to any variety which we have been able to find in the market and test. It is now widely grown in Maine. For the conditions of soil and climate in that state it is certainly to be regarded as the most highly "improved" variety known. Its origin and history are fully known, indeed are originally recorded in the archives of this laboratory.[30] All of the thousands upon thousands of bushels of this Maine 340 oat which were grown this year are the lineal, unchanged descendants of one particular oat plant which Dr. Surface isolated in 1910. That original plant has simply been multiplied, by seed, year after year without selection of any sort or kind, after the first isolation of the plant which originated the variety.

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[29] Coville, F. V., U. S. Dept. Agr. Bulletin 193, 1910; Circular 122, 1913; Bulletin 334, 1915.

[30] Cf. Surface, F. M., and Zinn, J., Me. Agr. Expt. Stat. Ann. Rept. for 1916, pp. 97–148.

The commercial variety of oats which comes the nearest under our conditions to equalling Maine 340 in yield and other desirable qualities is one known as the Early Pearl. The history of this variety has been given by Surface and Barber,[31] who got it from the originator, Mr. R. L. Copeland. Mr. Copeland says:

> The first seed was obtained from a bunch growing by the roadside some twenty years ago, presumably from one seed. It was examined and showed such merit that it was cut and preserved for seed. Although the first seed was not secured by me personally, it soon after came into my possession. The oat seemed to possess excellent qualities and as it matured fairly early and had a pearly tint to the hull I gave it the name of Early Pearl.

Since the beginning the oat has simply been grown by Mr. Copeland unmixed with other sorts.

Here again that painstaking and laborious selection, by which the practical breeder is supposed to make the wonderfully improved and valuable varieties which we have, is conspicuous by its absence. And one must not for a moment suppose that this oat is not a wonderfully superior one. Any oat which will yield, year in and year out, good seasons and bad, not less than about 80 bushels to the acre, and at the same time possess a whole series of other desirable qualities, which are too technical to go into here, is in the front rank of the products of the breeder's art. We find it to be surpassed only by some of our own new varieties. It outranks all other commercial varieties under our conditions.

Many other examples of the same sort of histories of varietal origin and improvement might be given. But de Vries[32] has covered the ground thoroughly and we need not stay longer over the plant side. The writer wishes to make clear before leaving the subject the reason for calling attention to these well-known matters. It is to emphasize that the "experience of practical breeders" shows that the principle of the gradual accumulation by continued selection of minute somatic variations has had no essential part in the origin or amelioration of certainly a great many of the best varieties of agricultural plants which we have to-day. The essential factors which have been involved in the production of our best fruits, grains, vegetables, flowers, etc., have been (1) the improved conditions of domestication, (2) mutations, leading at once to new and better forms, (3) hybridization, which by new combinations of characters and as a result of heterosis[33] has led to amelioration, and (4) the purification of previously mixed races or varieties by selective sorting. It is to the overwhelming importance of one or a combination of these factors that the ''experience of breeders'' points and not to Darwinian selection.

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[31] Surface, F. M., and Barber, C. W., Me. Agr. Expt. Stat. Ann. Rept. for 1915, pp. 137–192.

[32] de Vries, H., "Plant Breeding." Chicago, 1907.

But what of the animal side? Here the true facts are much more difficult to get at; in part for reasons which have been developed earlier in this paper, and in part for the reason that the making of new breeds of domestic animals is no longer going on to any extent except in the smaller sorts such as poultry. As has been pointed out elsewhere,[34] this is primarily a result of the great development of the system of pedigree registration, which puts a ban on cross breeding in cattle, horses, etc.

So then let us take as our first example one from poultry breeding where unequivocal facts are available. In his ''Organic Evolution'' Metcalf[35] makes the following statement:

> The extent of the modification produced by artificial selection is very great in many cases. Notice the common domestic chickens, in which the different breeds differ from one another to such a degree that if they occurred in nature the several kinds would be referred not only to different species, but to different genera. Compare the slender "game" which most closely of all resembles the ancestral "jungle fowl," with the heavy "Brahma" or "Cochin-china," or with the long-tailed "Japanese" cocks, or with the little "bantam."

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[33] East, E. M., and Hayes, H. K., U. S. Dept. Agr., Bur. Plant Industry, Bulletin 243, 1912.

[34] Pearl, R., ''Modes of Research in Genetics.'' New York, 1915.

[35] Metcalf, M. M., ''Organic Evolution.'' New York, 1904.

All these forms, according to Metcalf's idea, have been produced by selection from the jungle fowl. For a number of years past the writer has been interested in collecting evidence regarding the making of new races and varieties of bantams, for the purpose of seeing what part selection, in the Darwinian sense, probably plays in the matter. The problem was given enhanced interest and significance by the appearance of the important paper by Punnett and Bailey,[36] which showed that in respect of body weight bantams are differentiated from large fowls by at least three genetic factors, and that in a cross between a bantam breed (Seabright) and a larger breed (Hamburg) the inheritance of body weight is typically Mendelian. This latter result the writer had found to be true, using different breeds from those employed by the English workers, but had not worked out in detail the exact mechanism of the inheritance. New varieties of bantams are all the time being produced and exhibited at poultry shows. Broadly speaking, it is nearly true that for every different variety of large fowl a corresponding bantam variety either has been produced or is sure to be soon. In view of this great activity in the making of new varieties it seemed that an excellent opportunity was offered to find out how the expert bantam fancier really turns the trick. So the writer has corresponded with bantam fanciers in all parts of the world and in this way has accumulated a large amount of interesting material.

One question was always asked, and always in the same form. This was:

> Do you know of any case in which a stable race, variety or breed of bantams, which bred true indefinitely in respect to bantam size of body, was originated or created *solely by selection* of small sized individuals of a *large* race, variety, or breed of fowls, without any crossing in of bantam blood? If so, please give a detailed account of the circumstances.

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[36] Punnett, R. C., and Bailey, P. G., *Jour. Genetics,* Vol. IV, pp. 23–39, 1914.

The answers to this question were negative in every case except one. In that case the correspondent was unable to cite any specific instances illustrating his contention, but thought on general principles that it must be so. In other words, his belief in the selection theory, like that of Weismann, was based on wholly other grounds than demonstrative evidence. The general tenor of the answers to this question is well indicated by a statement of Mr. J. F. Entwisle,[37] who is probably the greatest authority on bantam breeds of poultry now living. He stated that it was thought by some that

> proper little bantams could be bred from large fowls without any admixture of bantam blood. . . . If such can be done, then our thirty-odd years' experience of bantam "manufacturing" counts for very little. We[38] have lived to see the manufacture of some forty varieties, and none without crossing, so far.

If time permitted, the citation of the detailed history of the making of several breeds of bantams would show very clearly that Darwinian selection plays an extremely minor and unimportant part in the process as it is actually performed. Large breeds of poultry show the same thing. Two of our most important breeds, the Wyandottes and the Orpingtons, are of comparatively recent origin. The facts as to their origin are well known and the essential biological factors concerned in both cases are the same, namely, hybridization as a start, followed by close inbreeding of desired segregating types. In other cases new varieties of poultry have appeared as sudden mutations by loss of factors. Such is the origin of the White Plymouth Rock and the White Cornish, for example.

## III. Selection Experiments

We now come to the third class of evidence on the selection problem, namely, that afforded by controlled *ad hoc* experimentation. Here the facts are so recent and so well known that a detailed review is unnecessary. I shall, therefore, only attempt to deal with them, for the most part, in a general way. Careful and critical selection experiments may be said in general to have given opposite results, according to whether the hereditary factors for the character which formed the basis of the selection were or were not positively known to be in a homozygous condition in all the individuals of the race experimented with. If the form used constituted a "pure line" in the strict sense of Johannsen's conception, so that every individual was surely known to be strictly homozygous for some state or condition of the character selected, and the mode of reproduction was such as automatically to retain and continue this condition, then the results of continued selection have in most cases been wholly negative so far as the production of any change in type is concerned. This is shown by the work of the Svälof Station[39] with various cereals, of Johannsen[40] with beans, of Jennings[41] with *Paramecium,* of Hanel[42] with *Hydra,* of Vilmorin[43] with wheat, of Ewing[44] with *Aphis,* of Surface and Pearl[45] with oats, of Fruwirth[46] with lentils, peas, soy-beans and lupines, of Lashley[47] with *Hydra,* of Agar[48] with *Simocephalus,* and of others.

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[37] Entwisle, J. F., *Poultry* (London), Vol. 30, p. 767, 1912.

[38] The ''we'' here is editorial. Mr. Entwisle is speaking of his own personal experience.

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[39] Cf. de Vries, H., *loc. cit. passim,* and Newman, L. H., "Plant Breeding in Scandinavia." Ottawa, 1912.

[40] Johannsen, W., "Ueber Erblichkeit in Populationen und in reinen Linien." Jena, 1902.

[41] Jennings, H. S., *Proc. Amer. Phil. Soc.,* Vol. 47, pp. 393–546, 1908; and AMER. NAT., Vol. 46, pp. 487–491, 1912.

[42] Hanel, E., *Jenaische Zeitschr.,* Bd. 43, pp. 321–373, 1908.

[43] Cf. Hagedoorn, A. L., and Hagedoorn, A. C., *Zeitschr. ind. Abst. Ver. Lehre.,* Bd. XI, pp. 145–183, 1914.

[44] Ewing, H. E., *Biol. Bul.,* Vol. 26, pp. 25–35, 1914; and *Ibid.,* Vol. 27, pp. 164–168; and *Ibid.,* Vol. 31, pp. 53–112, 1916.

[45] Surface, F. M., and Pearl, R., Me. Agr. Expt. Stat. Ann. Rept. for 1915, pp. 1–40.

[46] Fruwirth, C., *Zeitschr. f. Pflanzenzüchtung,* Bd. III, pp. 173–225, 1915.

[47] Lashley, K. S., *Jour. Exp. Zool.,* Vol. 19, pp. 157–210, 1915; and *Ibid.,* Vol. 20, pp. 19–26, 1916.

[48] Agar, W. E., *Phil. Trans. Roy. Soc.,* London, B, Vol. 205, pp. 421–489, 1914.

So far as the writer is aware the only important exceptions to the general rule exemplified by the above-cited researches are those obtained by Jennings[49] in *Difflugia,* and by his students, Middleton[50] with *Stylonychia,* and Stocking[51] with abnormalities in *Paramecium.* The facts in the case of these exceptions are beyond question. Just what their correct interpretation is does not seem to be so clear. Jennings himself (*loc. cit.,* p. 529) has expressed some doubt as to the significance of Miss Stocking's results so far as concerns their relation to normal reproduction. Morgan[52] has suggested that Jennings's *Difflugia* results may possibly be due to a sorting out of genetic diversities in the germ plasm, which came about from earlier conjugations, the material thus not representing a strictly homozygotic pure line. If this suggestion should prove to be valid the *Difflugia* work would fall at once into the same category as the cases of sorting out of pure lines from a mixed population by selection, with which the studies of Johannsen, de Vries and Jennings himself have made us familiar.

There is another point in connection with this extremely interesting and important investigation on *Difflugia* which seems to the writer, in the light of his own experience in breeding, of really extraordinary significance. One of the longest and most crucial selection experiments in the whole series was that for diverse numbers of spines in Family No. 326. During the first six periods after selection was begun in this experiment (p. 488) "no progress was made by selection." Then the basis of selection was changed. This change is described by Jennings in the following words (p. 489):

> After this time selection was based to a considerable extent on past performance. By this time many of the existent individuals had pro-

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[49] Jennings, H. S., *Genetics,* Vol. 1, pp. 407–534, 1916.

[50] Middleton, A. R., *Jour. Exp. Zool.,* Vol. 19, pp. 451–503, 1915.

[51] Stocking, R., *Jour. Exp. Zool.,* Vol. 19, pp. 387–449, 1915.

[52] Morgan, T. H., "A Critique of the Theory of Evolution." Princeton, 1916.

> duced several offspring. Where a parent of the low group had been found to bring forth high progeny, that parent was removed. Similarly, if a parent with a high number of spines is found to produce offspring with low numbers, this parent was removed. Thus in the low group we gradually tend to accumulate a set of individuals (1) which in the past have produced progeny with low numbers of spines; (2) whose ancestors for several generations back are individuals with low numbers of spines. In the high group the reverse conditions are fulfilled.

From the time this change in method was made until the end of the experiment, *selection produced a marked effect,* differentiating clearly high spine groups and low spine groups.

The significance of this result seems to me to lie in the fact that with the new method of selection described by Jennings the *ultimate basis of selection was changed from the soma to the germ.* Because after the change in method what *primarily* determined the selection of any particular individual for further reproduction was not its own spine number, but instead *its demonstrated ability to produce offspring with a particular spine number* (or nearly that number). A low spine parent was allowed to survive and reproduce not alone or primarily because it had few spines but only when in addition it was surely known to produce low spine progeny. This is indeed a different basis than that which merely selects individuals because of their somatic spine number and nothing else. It abruptly and completely transfers the selection from soma to germ. As has already been pointed out earlier in this paper (p. 5), there can be no question about the efficacy of selection which operates on a directly gametic rather than a somatic basis. This idea of making the basis of selection the ability to transmit to the progeny the desired quality is one which the writer has for a good many years strongly advocated as the only really useful or hopeful method in the practical breeding of higher animals. In his own work with poultry[53] it has been crowned with the highest practical success. Beyond doubt or question the reason for the success is because by this *method we select directly the kind of gametes we want.* In ordinary Darwinian selection we select the *kind of somata* we want, and trust blindly that a wise providence has implanted in them the sort of gametes we *need* in order to get further somata like those we selected. And as in so many other troublesome affairs in this vale of tears, too often we find in the outcome that our trust has been misplaced!

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[53] Pearl, R., AMER. NAT., Vol. XLIX, pp. 306–317, 1915.

It seems to me that whether Morgan's suggestion regarding the highly interesting and important results with *Difflugia* is true or not the *fact* dealt with in the preceding paragraph objectively parallels exactly the phenomena which one sees when he isolates pure lines from a mixed population (*e. g.,* in oats). He finds some individuals which are somatically what he wants but which fail to produce the sort of progeny he is looking for. These he discards. Others produce progeny which are like themselves. They transmit[54] their qualities and hence are retained.

Having considered the results of experiments on selection in pure lines we may turn to similar experiments with sexually reproducing organisms. Here the facts are, in the main, no less clear, but they are, on the whole, exactly opposite in their sense, at first sight at least. For in most of the experiments of this sort selection has been attended with an alteration of the type in the direction of the selection. This has been the case in the writer's[55] experiments on egg production, in the domestic fowl since 1908, in the work of Smith[56] and others with maize in

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[54] Lest there should be any misunderstanding I may say that I am fully aware that the old idea of heredity as a direct and material transmission of personal qualities from generation to generation is wholly incorrect, out-of date, and pedagogically pernicious. I find it, however, extremely convenient, saving of breath and good white paper, and, with this explanation, I hope permissible, to use ''transmit'' as a technical genetic term meaning ''to possess gametes of such sort as will produce in the progeny.''

[55] Pearl, R., AMER. NAT., Vol. XLIV, pp. 595–608, 1915.

[56] Smith, L. H., Ill. Agr. Expt. Stat. Bul. 128, 1908.

Illinois, in the work of Pearl and Surface[57] with maize, in MacDowell's[58] work on bristle number in *Drosophila*, in the work of Zeleny and Mattoon[59] with the bar eye of *Drosophila*, in the experiments of Castle and Phillips[60] with hooded rats, and in the work of some others. The difficulty with all these experiments is not in the facts but in their interpretation.

Before taking up this question of interpretation, however, it seems desirable to point out certain objective features which the results of these experiments have in common. The first is that they all occur (with the exception of the Jennings cases already discussed) in sexually reproducing organisms, not certainly known to be homozygotic with respect to all the factors which may be concerned in the production of the selected characters, and subject to a mixing of germ plasms in each generation. The second is that when any result at all follows selection in most if not all of the cases it comes quickly (*i. e.*, in a few generations), is relatively large in amount, and either no further change follows further selection or if it does occur it is again sudden and large in amount. This was true in the work with high producing lines of hens, of all work with maize by the ear-row method, and of MacDowell's with *Drosophila*, and also, as MacDowell[61] has so clearly demonstrated, in Castle's experiments with rats. A third point which strikes one is that in many of these successful cases of selection the basis of the selection has been fundamentally gametic, that of "progeny performance," rather than solely somatic. Individuals are selected for further multiplication which have demonstrated their ability to produce progeny bearing the desired somatic qualities. This was certainly the case in the Illinois corn work, as Surface[62] very clearly demonstrated. The writer[63] showed a number of years ago that it was the basis of success in selecting poultry for egg production. One strongly suspects it to be true in the other cases, though because the importance of the point has not been perceived, evidence in the published accounts is lacking on which to make any positive statement.

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[57] Pearl, R., and Surface, F. M., Maine Agr. Expt. Stat. Ann. Rept. for 1910, pp. 249–307.

[58] MacDowell, E. C., *Jour. Exp. Zool.*, Vol. 19, 1915.

[59] Zeleny, C., and Mattoon, E. W., *Jour. Exp. Zool.*, Vol. XIX, pp. 515–529, 1915.

[60] Castle, W. E., and Phillips, J. C., Carnegie Institution, Publ. 195, 1914.

[61] MacDowell, E. C., AMER. NAT., Vol. 50, pp. 719–742, 1916.

What is the correct interpretation of these favorable results? Two opposed opinions are held. Fortunately the heat of the controversy has been intense enough to produce some distillation and we at least have the issue very clearly and sharply defined. On the one hand it is held, because there has been an alteration of type in point of time coincident with successive selections, that selection on the basis of personal *somatic* qualities only, as such, in and of itself, has altered hereditary factors in the germ plasm. This view makes selection a cause of genetic variation,[64] a total reversal of the position held by Darwin and most of his followers. The opposing view is that selection can only be successful in altering the type when hereditary determiners to produce the desired somatic qualities are already present in the germ plasm. Selection, on this view, has nothing whatever to do with the causation of the variation, and is wholly powerless and without effect on the race unless either (*a*) the basis of the selection is directly gametic, by means of progeny performance test, or (*b*) the somatically selected individuals happen by good fortune to carry the necessary hereditary determiners in their germ plasm.

The opposition here really goes very far back. It is the world-old fight between heredity and environment, nature and nurture, germ and soma. One side believes first, that hereditary determiners or factors fluctuate regularly and frequently, if not indeed usually, and in high correlation with somatic characters; second, that mixing of germ plasms in fertilization alters hereditary determiners mutually and hence is, in and of itself, a cause of genetic variations, and, therefore, third, that a purely external agent, the continued selection of personal *somatic* qualities, will alter the germ plasm.[65]

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[62] Surface, F. M., IV$^e$ Conf. internat. de Génétique, Paris, 1911, pp. 221–235.

[63] Pearl, R., AMER. NAT., Vol. XLV, pp. 321–345, 1911.

[64] Castle, W. E., *Sci. Mo.*, Vol. 2, p. 91, 1916, and Castle, W. E., and Phillips, J. C., Carnegie Inst. Publ. 195, p. 31.

The other side believes first, that the *germ plasm* is fundamental and remarkably conservative, basing this belief on such observations[66] on the one hand as those of Walcott that pre-Cambrian annelids, snails, crustaceans, and algæ were in many cases so like forms living to-day as to belong to the same genera, though a period of time variously estimated at from 60 to 200 million years has elapsed; and, on the other hand, those of Wheeler on ants enclosed in amber two million years ago but morphologically identical with forms living to-day. It believes, second, that when the germ plasm changes it does so as a result either of wholly internal physiological causes, or of very extraordinary environmental stresses acting directly upon the germ cells; third, that mixing of germ plasms, in and of itself, does not mutually alter hereditary determiners, basing this belief on the regularity, constancy and cleanness of typical Mendelian segregation; and fourth, that selection only acts as a mechanical sorter of existing diversities in the germ plasm and not as a cause of alteration in it.

The alternative views have been presented. In the present state of knowledge nothing is to be gained by mere assertions of opinion as to which more nearly represents the truth. But one may at least advance the view, to which the whole of this paper has been leading, and which one may hope will be heartily concurred in by both sides in the selection controversy, that the great outstanding need in research on the problem of evolution in general, and of selection in particular, *is more, and more searching, investigations as to the causes of genetic (factorial) variation.* That both sides realize this need, and are all the time bending more and more energies to its selection, is indeed cause for congratulation and augurs well for the future of that branch of biological science in which America has taken a leading place.

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[65] In his last paper MacDowell has justly emphasized the scientific futility of defining and codifying the opponent's position in a controversy, so that one may the more neatly bowl him over. I am very sensible of the force of this point, and therefore have been at great pains in the preceding sentence to make only such statements as can be supported by verbatim quotations from the literature. Since, however, it seems to me equally important to keep the personal element out of scientific controversy, so far as may be, I do not make the specific references.

[66] Cited from Loeb, J., "The Organism as a Whole." New York, 1916.